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Received 24 May 2010; accepted 17 June 2010

Friend or foe: exotic flora and ecosystem function

Melanie Birtchnell[1] and Maria Gibson

Plant Ecology Research Unit, School of Life and Environmental Sciences
Deakin University, 221 Burwood Highway, Burwood, Victoria, 3125
[1]ecologist@optusnet.com.au

Abstract

Exotic flora, particularly weeds, are renowned for out-competing and displacing native flora, consequently affecting native fauna and pollinator relationships. Nonetheless, it stands to reason that weeds must provide some compensatory ecological value. This study assessed whether weeds are friend or foe to ecosystem function by considering the quality and quantity of pollen offered by widespread weeds in Australian ecosystems. Using the Honeybee *Apis mellifera* as a case study, and information derived from highly experienced commercial apiarists, we determined that 32 exotic plants are important pollen sources. Most species offered high to very high quality pollen. Pollen quality varied temporally, spatially and infraspecifically. Fifteen species were considered more beneficial to *A. mellifera* than others; only seven species were considered less beneficial. Thus, exotic flora contribute pollen resources that are valuable to maintain ecosystem function, particularly at times when flowering native species are few. (*The Victorian Naturalist* **127** (4) 2010, 124–136)

Keywords: exotic flora, weeds, ecosystem function, pollen, pollinators

Introduction

Exotic flora - globally - have a bad reputation. Their roll-call of maladies often includes out-competing and displacing native flora (e.g. Vitousek *et al.* 1987; Meiners *et al.* 2001; Levine *et al.* 2003) consequently affecting native fauna (Vitousek *et al.* 1987). Exotic species may interfere with native species further by affecting pollinator relationships, which can impact greatly on the ecology and evolution of native floral species (Ashman *et al.* 2004). We refer to those species most proficient at such maladies as weeds. Ubiquitous as weeds are, it stands to reason that they must provide some level of ecosystem service. Certainly, there are reports of the habitat values offered by weeds (e.g. Donald *et al.* 2001), although in many cases (including throughout Australia), exotic flora provide habitat for exotic fauna (Vitousek *et al.* 1987)!

Managing healthy ecosystems demands an understanding of which species provide high quality floral products and how temporal factors affect floral resources, for example, pollen quality and availability. Pollen quality usually is determined by nutritional levels (Keller *et al.* 2005) and a number of studies have investigated pollen quality in terms of nutrition, by analysing protein (Roulston *et al.* 2000; Somerville 1999; Somerville and Nicol 2006; Hanley *et al.* 2008), amino acid (Roulston and Cane 2000; Somerville and Nicol 2006), lipid (Todd and Bretherick 1942; Youssef *et al.* 1978; Day *et al.* 1990; Singh *et al.* 1999; Manning and Harvey 2002; Somerville 2005) and mineral composition (Herbert and Miller-Ihli 1987). These are important works and provide knowledge of the nutritional breakdown of pollens, but argument remains as to which nutritional components should be used to determine pollen quality (Keller *et al.* 2005).

The health of the highly organised, social Honeybee ('bee') *Apis mellifera* L. and hive health could be used to reflect pollen quality. Firstly, *A. mellifera* is farmed intensively in hives and observed closely by apiarists (beekeepers). Secondly, if pollen quality is poor, *A. mellifera* and hive health will deteriorate. If protein is insufficient, brood rearing decreases markedly (Kleinschmidt and Kondos 1976) and longevity is decreased (Sakagami and Fukuda 1968). Finally, apiarists have observed variation in pollen 'quality' and factors which may cause such variation over extended periods of time. These observations have been made over decades (often generations) and their livelihood has depended on accurate assessments of such variation. Thus, apiarists represent an alternative but important source of long-term observational data. Their understanding of pollen quality and quantity is critical to their livelihood. Their observations, therefore, are likely to be significantly more accurate and continuous than any other sources.

This study aimed to assess whether weeds are friend or foe to ecosystem functioning by considering the pollen quality and quantity offered by common, widespread weeds to Australian ecosystems. Using *Apis mellifera* as a case study, this paper also considered whether *Apis mellifera* displayed preferences for particular pollen sources. As these aspects are likely to affect native invertebrate (and, possibly, vertebrate) pollinators, the information obtained is of great importance in determining the ecological value of exotic pollen flora (that is, flora targeted for pollen). This was part of a larger study (Birtchnell 2008) which investigated the flowering ecology of south-east Australian melliferous (honey-producing) flora and used observational data from highly experienced, commercial apiarists to provide insight into otherwise difficult and time-consuming ecological examinations.

Methodology

The apiarists

Sixty-six apiarists were contacted and interviewed for the broader study into floral ecology. These 66 apiarists then were sent questionnaires relating to pollen quality and *A. mellifera* nutrition. The questionnaire consisted of 20 closed and open-ended questions pertaining to pollen flora. Only results relating to the exotic flora are presented here.

Apiarists resided in the Australian states and territories of (southern) Queensland, New South Wales, the Australian Capital Territory (ACT), South Australia, Victoria and Tasmania during their beekeeping years (Fig. 1); however, the migratory nature of Australian beekeeping often necessitates shifting hives interstate. This range defines the 'study area' (Fig. 1).

Each apiarist involved in this study had operated commercially for a minimum of 30 years and managed a minimum of 350 hives at any one time. This ensured apiarists had an intimate and long-term understanding of pollen quality and its variation, hive management and *A. mellifera* nutrition. Recruitment of apiarists who fulfilled the selection criteria was undertaken using two methods: first, the 'gatekeeper' approach (Berg 1999), whereby contact details for 11 apiarists were provided by the beekeeper who initially suggested the research concept; second, the 'snowball' technique (Gilbert 1993; Robson 1993), whereby each respondent was asked to provide details of other experienced apiarists. These techniques commonly are used in social research (e.g. Mesquita *et al.* 2001; Momartin *et al.* 2002; Poczwardowski and Conroy 2002) and employ existing interpersonal networks within closed communities and, in this case, a closed industry, to encourage participation in research (McLean and Campbell 2003). To ensure additional respondents were renowned for their expertise, each potential participant was recommended independently by at least two other participating apiarists. Participants were recruited and interviewed in accordance with Deakin University ethics requirements (Permit: EC92-2003).

Results

Thirty apiarists (45%) returned completed forms. This response rate was very good; normally, a 25% to 35% response is considered adequate (Somerville and Nicholson 2005). However, not all apiarists completed all questions. Thus, the sample size 'n' displayed in parentheses after results reflects the number of responses to *that* question, rather than the number of apiarists who returned the questionnaire (i.e. /30). For example, the notation [12/17] indicates that 17 apiarists answered the particular question and, of these 17 responses, 12 apiarists provided the same finding.

Pollen quality

Apiarists provided assessments of pollen quality for 32 exotic species, which belonged to 14 families (Table 1). The families most commonly represented were the Asteraceae, Fabaceae (six species each) and Rosaceae (five species) (Table 1). Pollen quality was assessed using a scale of one to five, where one reflected very low pollen quality and five reflected very high pollen quality. Whilst many species used for pollen were native (64%) (Birtchnell 2008), apiarists identified the exotic flora presented in Table 1 as vital in providing adequate pollen to maintain *A. mellifera* and colony health.

The vast majority of exotic flora offered mid-to-high quality pollen (Table 1). Most species that had an average rating of between four and five had a narrow range of ratings (usually between four and five) (Table 1). Most species were assigned a range of ratings by each apiarist who used them as a pollen source: for example, *Trifolium repens* was used by only one apiarist, yet was assigned a range of 3-5 (Table 1) thus highlighting that variation in pollen quality within a species can occur.

Pollen quality varied within a species (infraspecific variation) during a single flowering event (21/29), on a seasonal basis (in longer flowering species) (23/27) and from site to site (15/24) (Fig. 2). *Echium plantagineum*, *Brassica* spp., *Salix* spp., *Hypochoeris radicata*, *Taraxacum officinale* and thistles, in particular, were cited as having variable pollen quality (Table 1). Few apiarists provided comments relating to short-term infraspecific variation in pollen quality, but those who did considered temperature and rainfall to be most significant in determining pollen quality. Hot temperatures were considered detrimental but rainfall was beneficial. Budding/flowering intensity and soil type also were believed to affect pollen quality, but it is unknown whether these factors were detrimental or beneficial to pollen quality.

Approximately half of respondents (13/28) observed long-term variation in pollen quality in exotic species such as *H. radicata*. One respondent commented that all ground flora showed long-term variation; another two stated that all species varied depending on climate. Long-term variation in all species at some sites was observed by ten apiarists (10/29) - particularly the Victorian/South Australian mallee region and Maryborough in Central Victoria.

Fourteen factors that influenced rating of pollen quality were identified (Fig. 3) and most respondents (21/30) used more than one factor. Pollen colour, size and volume were considered important most often (Fig. 3) with taste and texture being less frequently cited (it should be remembered that the number of citations does not make one factor more or less important: one factor may have a greater influence in one site than another and particular factors may be easier to discern than others). *Apis mellifera* health and longevity, colony health, brood health and brood layout by the queen also were mentioned as important indicators of pollen quality but were cited by less than five apiarists (Fig. 3). Similarly, soil type, rainfall/soil moisture and seasonal variation were cited by less than five respondents (Fig. 3). For example, in deep sand (Fig. 3), *H. radicata* and *Medicago sativa* were cited as producing copious pollen of high quality which maintains vigorous *A. mellifera* brood health.

Pollen quantity and availability

Most apiarists found pollen was available throughout that species' flowering period (24/30). Three found that pollen was available either throughout the flowering period or only during part of the flowering period. Twenty apiarists found variation in the quantity of pollen available during flowering (20/29). Two apiarists commented that variable pollen quantity depended on the species, and were exhibited by some flora but not others. Yet another stated that less pollen was available at either end of the season. Twenty-six apiarists noted that *A. mellifera* began collecting pollen from a source as soon as flowering commenced (26/30) and 16 believed *A. mellifera* continued to do so until flowering in that species ceased (16/30).

The period of pollen collection usually was longer than the period of nectar collection (15/27). Five apiarists considered that nectar and pollen collection periods were similar (5/27), four that nectar collection occurred for a longer period (4/27) and three that the period of nectar and pollen collection varied (3/27). Sometimes, pollen collection commenced at the onset of flowering (2/30) while nectar yields commenced subsequently. Alternatively, pollen and nectar collection could slowly diminish together but sometimes both would cut out overnight (1/30), or pollen would remain to be collected when no nectar was available or *vice versa*. One respondent noted that nectar secretion stopped once pollination had occurred. Three respondents commented that nectar availability was controlled by temperature and rainfall.

Pollen preferences

Nearly all respondents believed *A. mellifera* display pollen preferences and, thus, have 'favourite' pollens/pollen sources (28/29). Eighteen exotic species were cited as being favourite pollen sources (Table 2). *Arctotheca calendula* pollen was cited most often (6/29) as being favoured by *A. mellifera*, followed by *Brassica napus* (5/29), *E. plantagineum* (5/29) and *Trifolium* spp. (4/29) (Table 2). All other species were cited less than four times each. Whilst the number of citations for each species may reflect the relative value and 'favour' displayed for floral sources by *A. mellifera*, it also may be indicative of the relative abundance of each species. Four apiarists commented that *Apis mellifera* preferred pollen sourced from species such as *Trifolium* spp., *E. plantagineum*, *A. calendula*, *Pyrus* spp. and *T. officinale* on the basis that they had higher protein content and resulted generally in large, healthy colonies. Indeed, these floral species were identified as producers of high quality pollen (Table 1) *and* as sources favoured by *A. mellifera* (Table 2), indicating that higher protein content may be the key to linking quality, preference and *A. mellifera* health.

The notion that *A. mellifera* have pollen preferences was supported further by a number of particular observations. For example, the native and ubiquitous *Eucalyptus camaldulensis* had abundant nectar *and* pollen yet *A. mellifera* visited the nearby *T. officinale*. Variation in the

Fig. 1. Map of Australia showing states/territories in which apiarists resided and extent of migratory range covered by this study ('study area'). Adapted from Australian Government.

Table 1. Pollen quality of exotic species on a scale of 1-5 (1 reflects a very low pollen quality and 5 a very high pollen quality). Species are presented in descending order of their average rating of pollen quality. Key to families (no. species in each family in parentheses): Ast – Asteraceae (6); Fab – Fabaceae (6); Ros – Rosaceae (5); Ger – Geraniaceae (1); Rut – Rutaceae (1); Bra – Brassicaceae (3); Asp – Asphodelaceae (1); Bor – Boraginaceae (2); Iri – Iridaceae (1); Cuc – Cucurbitaceae (1); Ona – Onagraceae (1); Sal – Salicaceae (1); Pin – Pinaceae (1); Poa – Poaceae (2).

Species	Family	Average pollen quality rating	Range of rating	Number of respondents citing species (n=30)	Number of respondents who consider pollen quality variable
Centaurea solstitialis L.	Ast	5	5	2	0
Ulex europaeus L.	Fab	5	5	2	0
Pyrus communis L.	Ros	5	5	1	0
Erodium cicutarium (L.) L'Her.	Ger	5	5	1	0
Citrus sinensis (L.) Osbeck, *Citrus* spp.	Rut	5	5	1	0
Trifolium spp.	Fab	4.9	4 to 5	9	0
Prunus dulcis (Mill.) D.A.Webb	Ros	4.8	4 to 5	5	0
Brassica rapa	Bra	4.6	4 to 5	6	0
Vicia faba L.	Fab	4.5	4 to 5	2	0
Trifolium fragiferum	Fab	4.5	4 to 5	1	1
Asphodelus fistulosus L.	Asp	4.4	4 to5	5	0
Echium plantagineum L.	Bor	4.1	2 to 5	14	1
Chondrilla juncea L.	Ast	4	4 to 5	3	0
Romulea rosea (Ewart) M.P.de Vos	Iri	4	4	2	0
Malus domestica Borkh.	Ros	4	4	1	0
Trifolium repens L.	Fab	4	3 to 5	1	1
Cucumis myriocarpus Naudin	Cuc	4	4	1	0
Arctotheca calendula (L.) Levyns	Ast	3.7	3 to 5	19	2
Rubus fruticosus spp. agg.	Ros	3.7	3 to 4	3	0
Medicago sativa L.	Fab	3.7	3 to 4	1	0
Brassica rapa ssp. *sylvestris* (L.) Janch.	Bra	3.3	1 to 5	6	0
Brassica napus L.	Bra	3.2	1 to 5	15	0
Thistles (Undet. spp.)	Ast	3.2	1 to 5	6	2
Taraxacum officinale Weber	Ast	3.2	1 to 5	5	0
Oenothera biennis L.	Ona	3	2 to 4	2	0
Heliotropium amplexicaule Vahl	Bor	3	3	1	0
Salix spp.	Sal	2.5	1 to 4	2	0
Hypochoeris radicata L.	Ast	1.9	1 to 4	7	0
Pinus radiata D.Don	Pin	1	1	3	0
Prunus sp. (Cherry)	Ros	1	1	1	0
Lolium perenne L.	Poa	1	1	1	0
Zea mays L.	Poa	1	1	1	0

preferred pollen source could occur within a single day, according to most apiarists (20/30). This principally was attributed to weather conditions (9/30) (Fig. 4) such as temperature, rainfall, wind and the occurrence of storms.

Pollen effects on A. mellifera health

Fifteen exotic pollen sources were considered more beneficial to *A. mellifera* than others (Table 3) but only seven were considered less beneficial (Table 4). Species considered to yield 'more beneficial' pollen were thought to specifically increase *A. mellifera* health, brood health, longevity and hive health (Table 3). Species considered less beneficial were believed to decrease only *A. mellifera* health and longevity (Table 4). Four species were included in both lists: *A. calendula*, *B. napus*, *T. officinale* and *M. sativa*, suggesting spatial and/or temporal variation affects pollen nutrition. *Actotheca calendula* was cited most often as being more beneficial (8/30), followed by *E. plantagineum* (7/30) (Table 3). Seven species were cited only once (Table 3), suggesting that these species provide lower quality pollen, have a more restricted distribution or are targeted by fewer apiarists due to extended intervals between flowering events or poor nectar production.

Brassica napus and *H. radicata* were cited most often as being producers of less beneficial pollen (3/30 and 2/30 respectively) (Table 4). Of the four species included in both the 'more beneficial' and 'less beneficial' lists, the majority were cited most often as 'more beneficial' (Tables 3 and 4). For example, *A. calendula* was cited eight times as producing more beneficial pollen (Table 3) and only once as being less beneficial (Table 4).

Apiarists observed that healthy *A. mellifera* were stronger, had greater stamina and were fatter. A healthy brood had greater vigour and filled a larger expanse of the frame (the component of the bee hive in which the queen lays eggs and where young bees are reared). Pollen produced by eight exotic floral species was of sufficiently high quality to improve brood health; seven species increased *A. mellifera* health, but only few species increased *A. mellifera* longevity (three species) and hive health (one species) (Table 3). In terms of detrimental impacts, only decreased *A. mellifera* health and longevity resulted from less beneficial pollen (three and one species respectively) (Table 4).

There was little difference in reports by apiarists as to whether one or multiple sources of pollen were *sufficient* to maintain hive health and to build hive populations; however, all but three stated that multiple pollen sources were *better*. This was attributed to multiple sources resulting in stronger *A. mellifera* individuals and colonies, individuals with stamina, increased longevity and improved brood rearing. It was believed that multiple pollen sources provided a more balanced diet and higher protein. Three respondents, however, stated that some single sources of pollen matched the benefits of multiple sources, for example, *Trifolium repens*, *T. fragiferum* and *E. plantagineum*.

Most apiarists stated that worker bees collect pollen from multiple sources (27/30). The proportion collected from each source varied and depended on:

- diversity of available pollen;
- quantity of pollen available;
- pollen composition;
- distance between apiary and pollen source;
- taste and requirement of the individual hive;
- time of day;
- season;
- weather (specifically temperature, rainfall, wind);
- duration of flowering;
- the prevalence/density of insects, presumably competing for floral resources.

If high quality pollen was available, *A. mellifera* collected mainly from that source, collecting only a small volume of pollen from other sources.

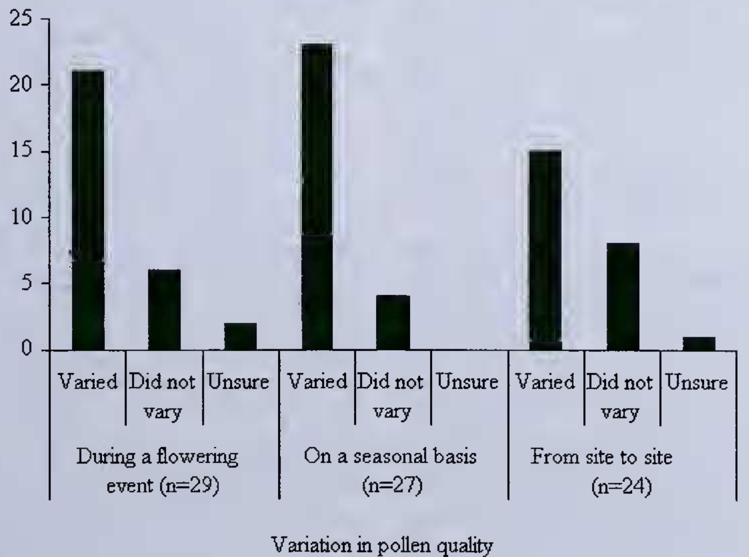

Fig. 2. Infraspecific variation of pollen quality in exotic and native flora

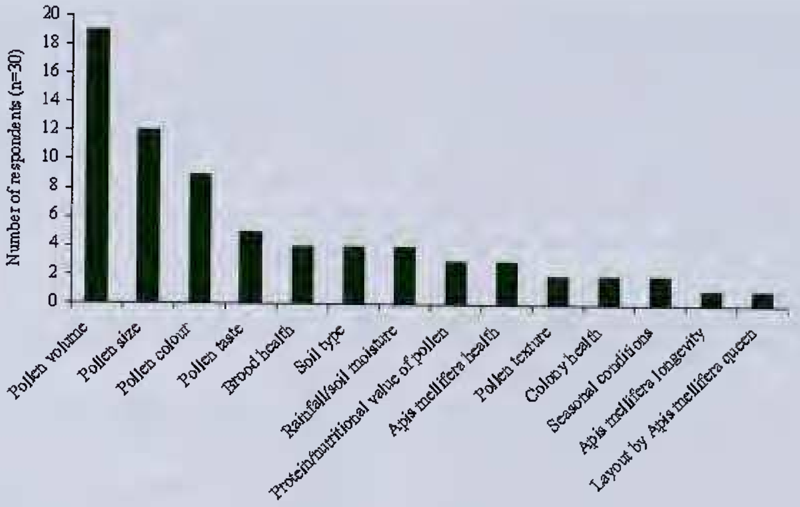

Fig. 3. Factors influencing rating of pollen quality.

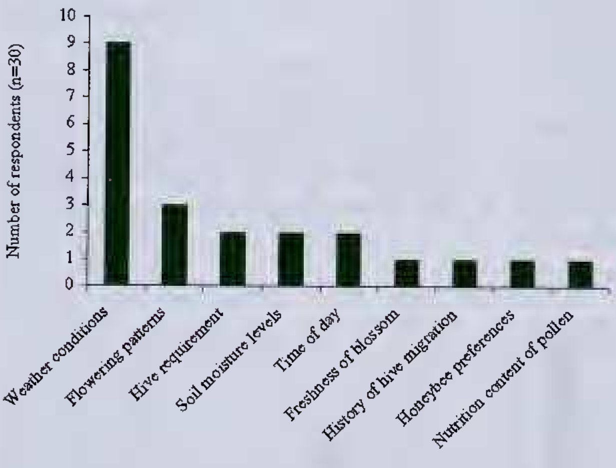

Fig. 4. Factors affecting daily preference for a pollen source

Discussion

More than one-third of the important pollen sources identified by apiarists were exotic species. Whilst this could be influenced by the availability of apiaries (sites where bee hives are 'parked') on or adjacent to exotic flora (for example, crops), it certainly reflects the extent to which *A. mellifera* is dependent on exotic pollen sources for pollen requirements. Whether this dependency on exotic pollen accurately reflects the extent to which *native* invertebrates (and vertebrates) are dependent on exotic pollen sources requires further investigation; nonetheless, this study has given valuable insights. Certainly, our ability to study the contribution of pollen sources is facilitated by the use of *A. mellifera* as it is a social insect and, so, brings pollen back to the hive where pollen 'traps' can be installed to remove pollen from returning bees, allowing analysis of pollen quantity and quality. Regrettably, analysis of pollen collected by non-social invertebrates and vertebrates, generally, is not so simple.

Apis mellifera keep only a small reserve of pollen within a hive at any one time (Pernal and Currie 2001) making *A. mellifera* and, consequently, their colony susceptible to short-term environmental variations in pollen quality and availability. In pollen-dependent species which are solitary (and, so, also keep only small reserves of pollen), this also would be pertinent and highlights the importance of a diverse floral community, to ensure temporal availability of floral resources such as pollen. Exotic plant species contribute to both floral diversity and pollen availability and, so, could be a vital resource for solitary pollen-dependent species when few native species (or crops) are flowering.

Pollen sourced from exotic flora is a vital resource for *A. mellifera,* and presumably also is critical for countless pollen-dependent vertebrates and invertebrates (e.g. Churchill and

Table 2. Pollen sources 'favoured' by *Apis mellifera*

Species	Number of citations (n=29)
Arctotheca calendula	6
Brassica napus	6
Echium plantagineum	5
Trifolium spp.	4
Prunus dulcis	3
Pyrus sp.	3
Salix spp.	2
Taraxacum officinale	2
All introduced ground flora	1
Brassica ?rapa	1
Brassica rapa ssp. *sylvestris*	1
Citrus sinensis	1
Hypochoeris radicata	1
Malus sp.	1
?Most ground flora	1
Trifolium fragiferum	1
Ulex europaeus	1
Vicia faba	1

? denotes species with unknown geographic origin

Christensen 1970; Turner 1984; van Tets and Hulbert 1999; Pestell and Petit 2007). The extent to which species utilise pollen and the range of pollen sources consumed, however, is incredibly variable. For example, Roulston and Cane (2000) conducted a comparison of the digestion of pollen in different animals and found that the percentage of pollen grains emptied by passing though the digestive tract ranged from 0% (a Honeyeater - bird) to 98.2% (*A. mellifera*) and varied depending on the floral source of the pollen. In another study, bat species that regularly consumed pollen extracted pollen cytoplasm (so, digested pollen) more efficiently than those bat species which did not consume pollen regularly (Herrera and Martínez del Rio 1998). Digestion of pollen by *A. mellifera* differs depending on the floral source (and the age of the bee), with pollen from some species possibly being digested by 'osmotic shock' (Kroon *et al.* 1974). In contrast, pollen from other sources such as *T. officinale* and *M. sativa*, both identified in this study as important and beneficial pollen sources, were digested slowly by degradation (Peng *et al.* 1985; 1986). Thus, in order to determine the potential nutritional value (i.e. effects on organism health and, so, ecosystem health) it would be necessary to know the biology of the species consuming the pollen *and* the nature of the pollen itself. Thus, the *actual* contribution of pollen to broader ecosystem health is difficult to quantify. Nonetheless, apiarists' observations of pollen sources, pollen quality and quantity, and the effects of different pollen on *A. mellifera* health show the important contribution exotic flora make to the pollen resource base.

Apiarists identified that the bulk of harvested pollen generally came from only a few plant species. This was expected as it also was observed in other studies (e.g. Synge 1947; Shawer 1987; Cortopassi-Laurino and Ramalho 1988). The three exotic species used most frequently were *A. calendula*, *B. napus* and *E. plantagineum*. Keller *et al.* (2005) reviewed about 25 studies and found *B. napus* ranked as one of the five top pollen sources globally. This is not surprising considering the abundance of this crop worldwide. It is likely that pollen from floral species identified in this study also provides critical nutrition to a range of native vertebrates and invertebrates, as these species also would benefit from high quality pollen. Thus, it is likely that the exotic species identified here are now important components of Australian ecosystems in terms of their role in maintaining population dynamics.

Apiarists assess pollen quality on a holistic basis. They observe whether detrimental effects occur, either immediately or with time, and so their assessment of pollen quality may not match those determined by chemical analyses. For example, pollen from some native species were considered excellent quality by apiarists (that is, they were rated > 4) (Birtchnell and Gibson 2006) but protein analyses suggest pollen from the same sources are of average quality (Somerville and Nicol 2006). This contrast in reports of pollen quality may highlight the underestimation of quality typical of chemical analyses of pollen collected by *A. mellifera* (Roulston and Cane 2000). Generally, chemical composition of pollen is reported on a per weight basis, thus reported values probably do not account for the added weight of the nectar or honey sugars which are added to the pollen by *A. mellifera* prior to transport. Therefore, it is likely that the concentration of chemical constituents in the pollen itself will be greatly underestimated in chemical analyses owing to the (highly variable) contribution made by nectar or honey to the pollen mass (Roulston and Cane 2000). Furthermore, spatial and temporal influences on harvested pollen may account for discrepancies between reported values. There-

Table 3. Impact of 'more beneficial' pollen on *Apis mellifera*. Species in bold were considered both more beneficial (Table 3) and less beneficial (Table 4).

Species	Increased *A. mellifera* health	Increased *A. mellifera* brood health	Increased *A. mellifera* longevity	Increased *A. mellifera* hive health	Number of respondents
Arctotheca calendula	X	X			8
Echium plantagineum	X	X	X		7
Brassica napus		X			6
Trifolium spp.	X		X	X	6
Brassica rapa	X	X	X		4
Prunus dulcis	X	X			3
Taraxacum officinale	X				2
Ulex europaeus					2
Asphodelus fistulosus		X			1
Chondrilla juncea	X				1
?Daisies (Asteraceae)		X			1
Medicago sativa					1
Pyrus sp.		X			1
Rubus fruticosus spp. agg.					1
Salix spp.					1

? denotes species with unknown geographic origin

Table 4. Impact of 'less beneficial' pollen on *Apis mellifera*. Species in bold were considered both more beneficial (Table 3) and less beneficial (Table 4).

Species	Decreased *A. mellifera* health	Decreased *A. mellifera* brood health	Decreased *A. mellifera* longevity	Decreased *A. mellifera* hive health	Number of respondents
Brassica napus	X		X		3
Hypochoeris radicata	X				2
Arctotheca calendula					1
Heliotropium amplexicaule					1
Medicago sativa	X				1
Oenothera biennis					1
Taraxacum officinale					1

fore, the way an apiarist assesses pollen quality may be more accurate than results determined by chemical analyses, as apiarists' observations are not necessarily affected by the relative ratio of nectar to pollen, but rather by the impact of the pollen pellets on *A. mellifera* health, longevity and other biological parameters, and are based on observations of pollen over an extended period rather than a single (or short-term) collection event.

The contrast in values of pollen quality reported in this study and those reported elsewhere also may result because apiarists consider quantity of pollen when determining quality. Thus, the *frequency* a pollen resource was cited by apiarists does not necessarily reflect its pollen quality. For example, *A. calendula* and *B. napus* were frequently cited yet protein analyses showed the first to be of poor quality and the latter of average quality (Somerville and Nicol 2006). A number of frequently used pollen sources, however, showed high protein contents, e.g. *E. plantagineum* and *Trifolium* spp. (Somerville and Nicol 2006).

It is well known that pollen quality varies amongst plant species (Somerville 2000; Keller *et al.* 2005). This study has identified that apiarists observed great variation in pollen quality *within* a species, with just under half the species cited being given different quality ratings (Table 1). The number of respondents who consider any one species to have a variable pollen quality, however, is extremely small (Table 1). Arguably, the variation observed by apiarists may exist because each has a different quality-benchmark; however, this is unlikely owing to the close-knit, interdependent nature of apiculture whereby apiarists often are reliant on the accurate observations made and reported by another beekeeper. It is probable, therefore, that infraspecific variation observed in pollen quality is spatial, thus influenced by environmental factors specific to location. Indeed, half the respondents agreed that site variation in pollen quality occurred and was found to influence other aspects of flowering ecology (Birtchnell 2002; Birtchnell and Gibson 2006; Birtchnell 2008). Somerville (2000; 2005) and Manning (2001) also showed that spatial variation in pollen quality could occur within a species.

A number of factors other than spatial influence were identified as responsible for differences in pollen quality within a species. Temperature and rainfall were considered significant influences over pollen quality: pollen quality reportedly decreased during high temperatures and/or low rainfall. Flowering intensity (levels of general budding) and soil type also were important. This has important implications for faunal and invertebrate dynamics and highlights the importance of landscape-scale resource availability in ensuring ecosystem fitness. Assessing budding/flowering intensity may be a good indicator of pollen quality as it easily is undertaken by apiarists, but quantitative data is necessary to determine whether this is a perceived or actual linear relationship. Similarly, it would be useful to compare pollen quality with chemical analyses of various soil types to quantify whether soil type provides a reliable surrogate for pollen quality. The Western Australian *Corymbia calophylla* (Lindl.) K.D. Hill & L.A.S. Johnson (Myrtaceae) produced pollen protein with higher amino acid and lipid levels when located on heavier soil types compared to the same species growing in sandy coastal soils (Manning 2001).

Other factors affecting pollen quality were timing within a flowering episode and within a season. Season could be a reflection of the different species in flower, a fact which is widely acknowledged in the literature (Keller *et al.* 2005), but it also could be a reflection of weather conditions. Hot, dry conditions were cited earlier as reducing pollen quality, so species flowering in summer might produce lesser quality pollen purely due to prevailing weather conditions. Variation within a single flowering episode also may be species dependent, as about 70% of respondents stated this was common. Some plant species were considered to have poor quality pollen at either or both the beginning of flowering and the end of flowering, whereas other species could produce poor quality pollen at any time of flowering. Causes for this were unknown and are difficult to explain. Poor quality pollen at the end of flowering seems logical, as soil resources could be depleted because of plant growth and competition, but at the start of flowering one would expect resources to be adequate if not better than at later stages of flowering. This could be due to changed rainfall patterns: apiarists have reported that rain is not falling at the seasonally-appropriate times (Birtchnell 2008) – many apiarists noted that this has affected flowering patterns and nectar production (Birtchnell 2008), and also may have affected pollen availability and quality. Research into potential implications of this is a matter of urgency.

Forty-three per cent of beekeepers believed there was long-term, infraspecific variation in pollen quality but 50% of beekeepers did not. This, again, could be due to site specific variables including the nature of the pollen resources available, especially as the majority of those who had observed such variation noticed variation within particular species such as *H. radicata* and between sites, particularly the Victorian mallee and central districts, which typically experience lower rainfall than elsewhere. Observed long-term variation in these dry areas, therefore, could be exacerbated further by reduced annual rainfall levels predicted to occur more commonly with climate change.

Almost all apiarists involved in this study believed *A. mellifera* had a favourite pollen source. A number of earlier studies demonstrated that *A. mellifera* colonies regulated pollen foraging in response to changing protein demands (e.g. Dreller *et al.* 1999; Fewell and Bertram 1999). Colony foraging increased in proportion to decreased pollen storage (Lindauer 1952; van Laere and Martens 1971). Experimental manipulation of stored pollen resulted in compensatory responses in terms of the numbers of foragers sent from the hive and subsequent rate of pollen collection (Camazine 1993; Dogterom and Winston 1999; Dreller *et al.* 1999; Fewell and Bertram 1999). Pernal and Currie (2001) extend this notion further and document that changes in foraging at the colony level occurred in response to deficits in either quantity or quality of pollen. This resulted from an increase in the proportion of foraging bees. The hive produced more foragers so an increased number of young, inexperienced foragers were sent out in response to quality and quantity deficits of pollen. These tended to collect larger loads of pollen and sample more widely as a result of a better energetic capacity (Pernal and Currie 2001). Older bees make compensatory responses for wing wear and degeneration of the flight mechanism (Cartar 1992; Pernal and Currie 2001). This study listed 18 species as favourite pollen sources of *A. mellifera* (Table 2), which is not surprising considering the breadth of area covered by apiarists who completed this survey. However, the number of species listed by any particular apiarist as favourites was small, usually between one and four species. That *A. mellifera* would prefer pollen with a higher nutritional content makes ecological sense as this would improve their health and longevity, enabling higher reproductive capacity and, in turn, ensuring the continuation of social structure (Wcislo and Danforth 1997), but there is some argument in the literature (Keller *et al.* 2005).

Although there is no direct evidence that *A. mellifera* display preferences, whether it be for pollen of higher nutritional content or not, indirect evidence has been presented in this study and also exists in the literature (Levin and Bohart 1955; Keller *et al.* 2005). For example, one apiarist observed that the native *E. camaldulensis* presented both abundant nectar and pollen, yet *A. mellifera* visited the exotic *T. officinale*. Why is this? Keller *et al.* (2005) demonstrated that different colonies at the same location would collect pollen from different sources. Preferences, however, were not fixed (van der Moezel *et al.* 1987). These results depended on the assumption of equal availability, but microhabitat changes may be influential, for example shading of hives might be slightly different, hence *A. mellifera* would delay foraging (Keller *et al.* 2005) and, therefore, may be presented with different pollen sources. Another explanation for pollen 'preferences' may deal with social behaviour, but these hypotheses need further investigation.

Generally, pollen from exotic flora was beneficial to *A. mellifera*. Whilst this may indicate that exotic flora are beneficial to other pollen-dependent species, extrapolating the effects of pollen quality on *A. mellifera* health to other pollen consumers is not straightforward. *Apis mellifera* uses a unique pollen collection system which involves mixing pollen with regurgitated nectar or honey to assist transport of pollen on their legs (Roulston and Cane 2000). These pollen 'pellets', therefore, are a mixture of nectar and pollen, which means that assessing the quality of the pollen component in isolation is complex. The floral source of nectar mixed with pollen is likely to change depending on availability and, possibly, on *A. mellifera* preference. Very little is known about what factors influence the amount of sugar (or the nutritional qualities) added to transported pollen – it could be dependent on pollen properties or, simply, the sugar concentration of the available floral source (Roulston and Cane 2000). Possibly, then, the addition of regurgitated nectar to pollen by *A. mellifera* may play a role in compensating nutritional value of deficient pollen, although this would be limited by the nutritional composition of available nectar and by the degree to which the pollen is deficient. Could this explain apiarists' observations of beneficial and less-beneficial pollen sources? This is an area for future research and may well provide additional information on ecosystem function and, particularly, resource dynamics for pollen-dependent species.

Conclusion

This study has summarised observations of apiarists pertaining to pollen sourced from exotic flora (and, thus, the potential contribution of exotic flora to ecosystem function) using *A. mellifera* as a case study. Whilst the surveys are an important source of observational data, they do not replace the necessity for verification with quantitative analyses. By using *A. mellifera*, itself an exotic species, we have demonstrated that the quality and quantity of pollen offered by common, widespread weeds is considerable, albeit variable. As well, we demonstrated that *A. mellifera* shows preferences for particular pollen and that exotic flora largely are beneficial for *A. mellifera* health. Whilst the use of *A. mellifera* is by no means a precise measure of the importance or otherwise of pollen from exotic sources for pollen-consuming vertebrates and invertebrates, it does allow observations of the impact of pollen on the health and longevity of a pollen forager, which would be difficult (if not, impossible) to observe in weaker social, or solitary, foraging species. Similarly, other strongly social invertebrates rarely are 'farmed', so, are not commonly observed nor manipulated in such an intensive manner. *Apis mellifera* is unique in that it can be managed and observed in 'free-flying', uncaged experiments and may provide critical insights into a host of pollen-dependent ecosystem dynamics. Rightly, exotic flora in Australia are renowned for acting as foe to ecosystem function in many ways; however this study has illustrated that existing exotic species may act somewhat as a friend to native ecosystems by offering high quality, relatively abundant pollen resources when pollen from native floral sources otherwise is low.

Acknowledgements

We extend our gratitude to the apiarists who donated their expertise and time to this study. Thanks to Stephen Doughty for producing a stellar map. Sincere thanks to Steve Asirvadem and Glenda Birtchnell who donated their time to facilitate preparation of this manuscript. An anonymous reviewer provided very helpful comments – thank-you. This study was funded by the Rural Industries Research and Development Corporation (RIRDC) and Deakin University, and was completed whilst MB was the recipient of an Australian Postgraduate Award.

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Received 17 June 2010; accepted 24 June 2010

Mature and agressive 'Active Outbreak' of Bluebell Creeper at Windy Hill Native Forest Reserve, Mount Burr Range, SA, where the seed-bank from a long-established infestation was inadvertently germinated through a prescribed burn. Bluebell Creeper now dominates the understorey of this woodland, and forms part of the largest known outbreak of the weed in south-eastern Australia. Photo by Mark Bachman; see article on page 137.